

TAXONOMIC OBSERVATIONS ON THE NORTH AMERICAN SPECIES OF HORDEUM

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In his "Manual of the Grasses of the United States," A. S. Hitchcock (1935) recognized in the genus *Hordeum* eight species and four varieties. Since no species occur in Canada, Mexico, or Central America which are not also found in the United States, this treatment included all of the North American species of the genus which Hitchcock recognized. Closer examination of the morphology and the cytology of these species has shown his treatment to be inadequate.

In this paper, some modifications of Hitchcock's taxonomic treatment of the genus are given, including the description of three new species.

The conventional morphological characters used in the classification of the Gramineae are sometimes insufficient for the identification of the species of *Hordeum*. Characters of the spike, glumes, lemmas, anthers, leaves, etc. are often very similar in distantly related species, and, in addition, the variation between species often is confounded by qualitative and quantitative intraspecific fluctuation. The presumably allopolyploid character of many of the species is largely responsible for this pattern.

The proper taxonomic treatment of this genus was realized by Hauman (1916) when he pointed out: ". . . une monographie, même partielle, du genre *Hordeum* ressort sans doute encore de la botanique de l'avenir, dont la systématique devenue expérimentale, se sera transformée en une réelle investigation phylogénique basée sur l'observation, en culture, de la constance et de l'hérédité des caractères."

The structure of the epidermal cells of the leaves has been a valuable character for the differentiation of some species. These observations were based on the work of Prat (1932), who emphasized the importance of such a complex tissue in the taxonomic arrangement of the grasses.

For the identification of species of *Hordeum*, the following characters of the epidermis of the blade must be taken into consideration: (a) form of walls of elongate cells; (b) presence or absence of paired siliceous and suberized cells; (c) disposition of siliceous cells in the nerves; (d) size of stomata. These characters can be easily observed by diaphanizing a little piece of the blade, heating it with a crystal of phenol, removing the excess of liquefied phenol, and mounting in Canada balsam or similar media. With this treatment the siliceous cells become reddish (Johansen, 1940: 198).

Although the characters mentioned are rather constant in

all the leaves of the adult plant, the observations were made in the middle part of the second leaf below the spike.

In relation to the cytological evidence, all the species of *Hordeum* studied have the basic chromosome number $x = 7$, and the chromosomes are not conspicuously differentiated from each other, except that two pairs possess satellites, as was observed in both diploid and tetraploid species. However, the number of chromosomes has been valuable for clarifying the interrelationship of several species, and the recognition of diploid and tetraploid forms in a complex has allowed further segregation of

Table 1. CHROMOSOME NUMBERS IN NORTH AMERICAN SPECIES OF *HORDEUM*

Species	Chromosome number (2n)	Count made by
<i>H. californicum</i>	14	Stebbins & Love (sub <i>H. nodosum</i> , pro parte) Chin (sub <i>H. nodosum</i> , pro parte)
<i>H. Hystrix</i>	14	Covas
	28	Chin (sub <i>H. Gussoneanum</i>)
<i>H. marinum</i>	14	Ghimpu, Griffée, Wulff
<i>H. murinum</i>	14	Ghimpu, Perak, Stolze
	28	Andres, Chin, Griffée, Stählin, Aase and Powers
<i>H. pusillum</i>	14	Andres, Chin, Kihara, Perak
<i>H. Stebbinsii</i>	14	Covas
<i>H. vulgare</i>	14	Griffée, etc.
<i>H. brachyantherum</i>	28	Stebbins & Love (sub <i>H. nodosum</i> , pro parte) Chin (sub <i>H. nodosum</i> , pro parte)
<i>H. depressum</i>	28	Covas
<i>H. jubatum</i>	28	Andres, Chin, Griffée, Perak, Stählin, Stebbins and Love
	14	Tanzi
	ca. 14	Brown
<i>H. leporinum</i>	28	Perak

species on the basis of morphological characters neglected thus far.

The number of chromosomes of species of *Hordeum* recently has been compiled by Darlington and Janaki Ammal (1945) and by Myers (1947). Table 1 gives all of the chromosome numbers found in North American species of *Hordeum*. Those counts made by myself are given in boldface; counts made by other authors are given as cited by Myers.

All the North American species, except *H. arizonicum* and *H. murinum*, were observed in culture. Many interspecific crosses were attempted and some of them have been successful; this material will be the object of further cytogenetic studies.

I wish to acknowledge appreciation to Dr. G. L. Stebbins, Jr., Division of Genetics, University of California, Berkeley, at whose suggestion this study was elaborated, for helpful advice and criticism. Also, I am indebted to the curators of the following herbaria for the loan of material: Gray Herbarium, Harvard University (GH); New York Botanical Garden (NY); United States National Herbarium (US); California Academy of Sciences (CAS); Dudley Herbarium, Stanford University (DS); University of California, Berkeley (UC); Grass Herbarium of the Agronomy Division, University of California, Davis (UC-D); Herbarium of Mr. A. Ruiz Leal, Mendoza, Argentina (Leal). The abbreviations used, insofar as possible, are those proposed by Lanjouw (1939).

TAXONOMIC TREATMENT

The species of *Hordeum*, native or naturalized in North America, can be recognized by means of the following key, in which is included *Hordeum nodosum*, an exclusively Old World species, which repeatedly has been reported as growing in both North and South America.

KEY TO THE NORTH AMERICAN SPECIES OF HORDEUM

A. Perennials.

- B. Auricles small (0.2–1.5 mm. long) but usually present; elongate epidermal cells of the leaf blade with undulate walls (fig. 1); paired siliceous and suberized cells in the epidermis of the blade frequent; lodicules 1.3–1.9 mm. long; anthers 2.8–4.3 mm. long; Old World..

H. nodosum

- BB. Auricles obsolete or absent; elongate epidermal cells of the leaf blade with straight walls; epidermis of the blade without paired siliceous and suberized cells; lodicules less than 1.3 mm. long; anthers 1–3 mm. long; native in North America.

- C. Glumes and awns 1.8–8 cm. long..... 3. *H. jubatum* including var. *caespitosum*

- CC. Glumes and awns less than 1.8 cm. long.

- D. Leaves pubescent, 1.5–5 mm. wide; siliceous cells in the nerves of upper epidermis of blades usually isolated or forming short stripes; pedicels of lateral spikelets erect, almost straight (fig. 5, left); glumes of central spikelet $1\frac{1}{2}$ to $2\frac{1}{2}$ times as long as the palea; prolongation of rachilla usually very short or wanting; anthers usually 1.5–3 mm. long; diploid species; California..

1. *H. californicum*

- DD. Leaves usually glabrous, sometimes scabrous or shortly pubescent, 3–9 mm. wide; siliceous cells in the nerves of upper epidermis of blades forming rather continuous stripes, only inter-

rupted by hair- or apiculated-cells; pedicels of lateral spikelets usually curved (fig. 5, right); glumes of central spikelet often scarcely longer than the palea; prolongation of rachilla usually well developed; anthers usually 1-1.5 mm. long; tetraploid species; widespread in boreal and western North America

2. *H. brachyantherum*

AA. Annuals.

E. Glumes of central spikelet and the inner ones of lateral spikelets with ciliate margins.

F. Floret of central spikelet sessile or subsessile, its lemma, awn and palea all longer than those of the lateral spikelets; inner glumes of lateral spikelets narrower than those of the central spikelet; palea of lateral florets almost glabrous; diploid species

10. *H. murinum*

FF. Floret of central spikelet borne on a pedicel usually as long as the pedicels of the lateral spikelets, its lemma, awn and palea all shorter than those of the lateral spikelets; inner glumes of lateral spikelets as broad as those of the central spikelet; paleas of lateral florets pubescent.

G. Spike very dense (6-8 spikelets per cm. of rachis); rachis with ciliate margins; the cilia 0.25-0.75 mm. long; prolongation of rachilla of lateral spikelets 1.0-2.2 mm. long, rather stout; stamens of central florets included at anthesis, their anthers 0.2-0.5 mm. long, entire or shortly lobed at the base, their filaments without starch grains; diploid species

9. *H. Stebbinsii*

GG. Spike not very dense (3-5 spikelets per cm. of rachis); rachis with margins scabrous or very shortly ciliate, the cilia 0.1-0.3 mm. long; prolongation of rachilla of lateral spikelets 2.8-3.7 mm. long, rather slender; stamens of central florets exerted at anthesis, their anthers 0.8-1.5 mm. long, with strongly bilobed base, their filaments containing conspicuous starch grains which become strongly colored in iodine solution; tetraploid species

11. *H. leporinum*

EE. Glumes not ciliate.

H. Auricles very long; rachis continuous; all three spikelets sessile, fertile

12. *H. vulgare* f. *hexastichon*

HH. Auricles obsolete or wanting; rachis articulate; lateral spikelets pedicelate, usually neuter.

- I. Inner glumes of lateral spikelets strongly broadened, 0.6–1.8 mm. wide.
 - J. Spike ovate, usually less than 4 cm. long; awns strongly spreading; introduced from the Old World..... 4. *H. marinum*
 - JJ. Spike linear-oblong, usually over 4 cm. long; awns and glumes suberect; native to North America..... 6. *H. pusillum*
- II. All glumes linear-subulate, less than 0.6 mm. wide.
 - K. Spike ovate to ovate-oblong, usually less than 5 cm. long; awns and glumes strongly spreading at maturity; bases of glumes of lateral spikelets prominent above the pedicel, both inserted at almost the same level; lodicules glabrous; diploid species introduced from the Old World.. 5. *H. Hystrix*
 - KK. Spike linear-oblong, usually over 5 cm. long; awns and glumes suberect; bases of glumes of lateral spikelets not prominent above the pedicel, the inner one inserted at a lower level than the outer; lodicules ciliate at margins; polyploid species native to North America.
 - L. Central spikelet 13–22 mm. long including awn; pedicels of lateral spikelets almost straight; lateral florets with acute but awnless lemmas; tetraploid species; California, Oregon, Idaho, Washington, British Columbia.. 7. *H. depressum*
 - LL. Central spikelet 26–32 mm. long including awn; pedicels of lateral spikelets curved; lateral florets with acuminate, very shortly awned apex; hexaploid (?) species; Arizona, southeastern California 8. *H. arizonicum*

1. *Hordeum californicum* Covas et Stebbins, sp. nov. *H. nodosum* auct. americ. non L., pro parte.

Perenne caespitosum; culmi erecti 20–65 cm. alti. Folia viridula vel glauca; vaginae inferiores pilosulae, superiores glabrae; ligula truncata, 0.15–0.4 mm. longa; lamina 1.5–5 mm. lata, pilosulae, basi exauriculata. Spica 2.5–8 cm. longa, 0.4–0.7 cm. lata aristis non computatis; articulis rachiae elongatis, margine ciliatis. Terniorum spicula intermedia sessilis, 12–22 mm. longa

aristis computatis; glumae setaceae, scabrae, 8–17 mm. longae, 0.08–0.2 mm. latae; glumella glabra, in parte superiore scabra; palea 5.5–9.5 mm. longa, acuminata, in parte superiore scabra; antherae 1.5–3 mm. longae. Spicula laterales pedicellatae, neutrae vel ♂ vel ♀; pedicellis erectis, gracilib; glumis setaceis, scabris, 0.1–0.18 mm. latis; glumella subulata vel lanceolata, scabra. Chromosomae $2n = 14$.

Perennial with tufted, erect culms 20–65 cm. tall. Leaves bright green or glaucous, the basal ones with retrorsely pubescent sheaths, the upper ones with glabrous sheaths; ligule truncate 0.15–0.4 mm. long; blades 1.5–5 mm. wide usually pubescent on both surfaces (the hairs usually ascending, short and stout to long and slender); elongate epidermal cells of the blade with straight walls; siliceous cells in the nerves of upper epidermis usually isolated or forming short stripes; auricles wanting or vestigial. Spike linear-oblong, green or purplish, 2.5–8 cm. long, 0.4–0.7 cm. wide without awns; rachis articulate, with usually elongate segments ciliate at the margins. Central spikelet sessile, 12–22 mm. long including awn; glumes setaceous, scabrous, 8–17 mm. long, 0.08–0.2 mm. wide; lemma usually glabrous, scabrous toward apex, sometimes hispid-pubescent, tapering into an awn 7–15 mm. long; palea 5.5–9.5 mm. long, usually acuminate, scabrous toward apex; anthers 1.5–3 mm. long; prolongation of rachilla wanting or commonly weak and not reaching the middle of palea. Lateral spikelets pedicellate, the pedicels slender, almost straight, 1–1.8 mm. long; glumes setaceous, scabrous, 0.1–0.18 mm. wide, usually parallel in the basal portion; floret commonly neuter, sometimes staminate or perfect, 3.5–9 mm. long; lemma commonly subulate, scabrous; palea frequently wanting. Modal diameter of pollen grains 32–36 μ . Modal length of stomata 30–34 μ . Chromosome number $2n = 14$.

Type. Grassy pasture, in alluvial soil from shale and granitic formations, altitude 1700 feet (520 m.); foot of Haystack Hill, Hastings Reservation, Jamesburg, Monterey County, California, May 15, 1948, *G. L. Stebbins 3944* (UC 754600; isotypes, NY, GH, US, DS, UC-D).

Specimens examined. CALIFORNIA. San Diego County: Palomar Mountain, *Orcutt* (DS 190554). San Miguel Island: head of Willows Canyon, *Hoffmann* (UC 675632). Santa Barbara County: Santa Barbara, *Elmer 3939* (GH, DS); Point Sal west of Guadalupe, *Beetle 1927* (UC-D). San Luis Obispo County: Rancho Asuncion, Templeton, *Burt Davy 7600* (UC); San Luis Obispo, *Stebbins 3357* (UC); 1 mile north of Moro Beach, *Wiggins 3605* (DS); roadside near San Luis Obispo, *Condit* (UC 454-061); Cholame, without collector (UC 337742). Monterey County: summit of Jolon Grade, *Ferris 8422* (GH, UC, DS); 11½ miles east of Jamesburg, *Stebbins 3415* (UC); Pacific Grove, *Heller 6703* (GH, DS); 2½ miles north of Lynch Ranch, *Graham 393*

(UC); mouth of Garrapata Creek, *Ferris 3709* (DS); Tassajara Hot Springs, *Elmer 3315* (DS); 2 miles south of Monterey, *Steb-*

TABLE 2. DIFFERENTIATING CHARACTERISTICS OF *HORDEUM NODOSUM*, *HORDEUM CALIFORNICUM*, and *HORDEUM BRACHYANTHERUM*.

	<i>H. nodosum</i>	<i>H. californicum</i>	<i>H. brachyantherum</i>
Chromosome number (2n)	28	14	28
Leaf blade	Rather stiff, glabrous to pilose, 1-5 mm. wide	Rather soft, pubescent, 1.5-4 mm. wide	Rather soft, usually glabrous, 3-9 mm. wide
Auricles	Usually present	Wanting or vestigial	Wanting or vestigial
Walls of elongate epidermal cells of leaf blade	Undulate	Straight	Straight
Paired siliceous and suberized cells in the epidermis of leaf blade	Present	Absent	Absent
Siliceous cells in the nerves of upper epidermis of leaf blade	Usually isolated or forming short stripes	Usually isolated or forming short stripes	Usually forming long stripes
Ratio (length/maximum width) of the segments of rachis	2-3	2-3	1.2-2.2
Ratio (length of glumes of central spikelet/ length of palea)	1.0-1.2	1.5-2.5	1.2-1.8
Prolongation of rachilla of central spikelet	About as long as the middle of the palea	Usually wanting or not reaching the middle of the palea	Usually surpassing the middle of the palea
Length of anthers (mm.)	2.8-4.5	1.5-3	1-1.8
Length of lodicules (mm.)	1.3-1.9	0.7-1.1	0.7-1.1
Pedicels of lateral spikelets	Usually straight	Usually straight	Usually curved
Lemma of lateral floret	Usually hispid toward apex	Usually scabrous	Usually scabrous
Modal length of stomata (μ)	44-50	30-34	42-48
Modal diameter of pollen grains (μ)	39-44	32-36	39-44

bins 3437 (UC, GH, US); 6 miles east of Carmel, *Stebbins 3435* (UC, US). San Benito County: trail to Hepsedam Peak, *Dudley* (DS 18633); New Idria, *Dudley* (DS 18640). Santa Clara

County: Saratoga, *Pendleton 1456* (UC-D). Mount Hamilton Range, Stanislaus County: junction of Adobe Creek with Arroyo del Puerto Creek, *Sharsmith 3760* (UC); Adobe Creek, *Sharsmith 3606* (UC); Colorado Creek, *Sharsmith 3176* (UC). San Mateo County: Spring Valley, *Demaree 9144* (GH). Alameda County: Codornices Park, Berkeley, *Stebbins 3411* (UC, NY, US); Berkeley hills, *Long 166a* (UC). Tuolumne County: Long Gulch near Rawhide, *Williamson 226* (DS). Marin County: San Anselmo Canyon, *Howell* (CAS). Napa County: road from Rutherford to Monticello, *Stebbins* and *Covas 3933* (UC, GH). Sacramento County: $\frac{1}{2}$ mile west of Scott Ranch, *Nordstrom 5703* (UC). Lake County: 2 miles north of Middletown, *Wolf 1899* (DS); $2\frac{1}{2}$ miles northeast of Middletown, *Stebbins* and *Covas 3922* (UC, GH, NY, US); north side of Cobb Valley near Glenbrook, *Tracy 14017* (GH). Mendocino County: Sherwood Valley, *Burt-Davy* and *Blasdale 5179* (UC); Ukiah, *Burt-Davy* and *Blasdale 5021* (UC).

This new species was referred previously to *H. nodosum* L. (see key and table 2 for differential characters). Stebbins and Love (1941) and Chin (1941), independently, found diploid forms in the complex called *H. nodosum*; those forms correspond now to *H. californicum*, while the tetraploid forms must be referred to *H. brachyantherum* Nevski (= *H. boreale* Scribn. & Smith). *Hordeum californicum* was subsequently recognized as a different species by Dr. Stebbins (verbal communication) on the basis of the differences between the spontaneous tetraploid forms and the artificially produced tetraploid.

Hordeum californicum and *H. brachyantherum* are two closely related species, which often are difficult to separate. However they must be regarded as different species, on the basis of the following facts:

- a) Although there is no single morphological character which absolutely differentiates the two species, a combination of several characters defines them fairly accurately. The main differential characters are shown in table 2. Perhaps the best distinctive character is the disposition of the siliceous cells in the upper epidermis of the leaf blade.
- b) The different chromosome number is an effective barrier

EXPLANATION OF THE FIGURES. PLATE 1.

PLATE 1. NORTH AMERICAN SPECIES OF HORDEUM. FIG. 1, *H. nodosum*, lower epidermis of leaf blade, $\times 290$ (*Kneucker 535*). FIG. 2, *H. brachyantherum*, upper epidermis of blade, the siliceous cells in black, $\times 235$ (*Stebbins 2747*). FIG. 3, *H. californicum*, upper epidermis of blade, the siliceous cells in black, $\times 235$ (*Stebbins 3437*). FIG. 4, lateral spikelets, $\times 7$: left, *H. depressum* (*Beetle 4373*); right, *H. Hystrix* (*Beetle 2954*). FIG. 5, bases of spikelets, ventral side, $\times 10$: left, *H. californicum* (*Stebbins 2734*); right, *H. brachyantherum* (*Stebbins 3103*). FIG. 6, *H. Stebbinsii*, chromosome complement, late diakinesis, $n=7$, $\times 1075$ (from near Davis, Yolo County, California). FIG. 7, *H. depressum*, chromosome complement, somatic cell, $2n=28$, $\times 1210$ (from near Concord, Contra Costa County, California).

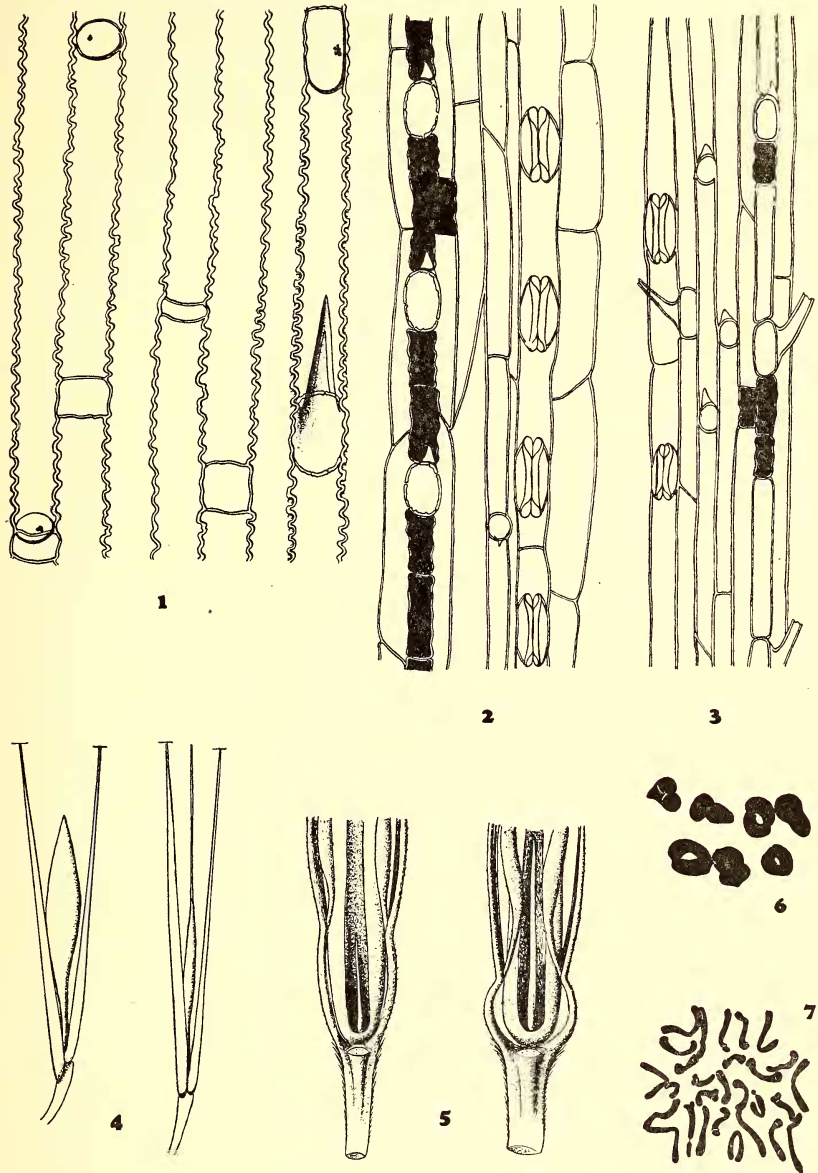


PLATE 1. NORTH AMERICAN SPECIES OF HORDEUM.

against the interchange of genes between the two species. In attempts to make artificial hybrids between *H. californicum* and *H. brachyantherum* only five seeds were obtained in more than two hundred cross-pollinated florets.

c) The tetraploid produced artificially by Dr. Stebbins from *H. californicum* (by use of colchicine) is similar to this species in qualitative characters, differing only in the larger size of cells and vegetative and reproductive organs.

d) The geographic distributions of *H. californicum* and *H. brachyantherum* follow a quite different pattern. *Hordeum californicum* occurs in the interior coast ranges of northern California, reaching the coast in central and southern California; occupies hills, slopes, stream sides, usually in not very heavy soil and not in alkali or saline areas. *Hordeum brachyantherum*, in California, grows in the mountains and along the coast and is a plant of bottom lands, often in sub-alkaline soils. Sometimes (in Lake County, Alameda County, etc.), the two species grow in neighboring areas, but there they occupy different habitats and show no sign of intergradation.

A fact which provides a good basis for explaining the nature of the interrelationship between *H. californicum* and *H. brachyantherum* is that this last species often approaches *H. californicum* in its morphological characters, while *H. californicum* is a less variable species which never looks like the typical *H. brachyantherum*. Thus it is not risky to assume that *H. brachyantherum* is an allopolyploid derived from *H. californicum* and some undetermined diploid species. A similar pattern of mutual variation was pointed out by Anderson (1936) in the case of *Iris virginica* and its derivative *Iris versicolor*.

2. *HORDEUM BRACHYANTHERUM* Nevski in Acta Inst. Bot. Acad. Sci. U.R.S.S. 1(2): 61. 1936. Based on *H. boreale* Scribn. & Smith in U. S. Dept. Agric. Bull. Agr. 4: 24. 1897. Non Gandoger in Bot. Not. 1881:157. Hultén, Flora of Alaska and Yukon, in Lund, Univ. Årssk. N. F. Avd. 2 Bd. 38, 1: 265. 1942. *H. nodosum* var. *boreale* (Scribn. & Smith) Hitchcock in Am. Jour. Bot. 21: 134. 1934, type locality: Atka Island, Aleutian Islands. *H. nodosum* auct. americ. non L., pro max. parte.

This species, like the preceding one, was referred by many authors to *H. nodosum* L. Both species are tetraploid, but there

EXPLANATION OF THE FIGURES. PLATE 2.

PLATE 2. NORTH AMERICAN SPECIES OF HORDEUM. FIG. 8, *H. Stebbinsii*, spikelets, ventral side, $\times 3$ (from the type). FIG. 9, *H. leporinum*, spikelets, ventral side, $\times 3$ (Burt-Davy 1685). FIG. 10, *H. murinum*, spikelets, ventral side, $\times 3$ (Muenscher 5658). FIG. 11, *H. arizonicum*, spikelets, $\times 4$ (from the type). FIG. 12, prolongation of rachillas of lateral spikelets, $\times 6$: left, *H. Stebbinsii*; center, *H. leporinum*; right, *H. murinum*. FIG. 13, *H. Stebbinsii*, anther of central floret, $\times 60$. FIG. 14, *H. leporinum*, anther of central floret $\times 60$.

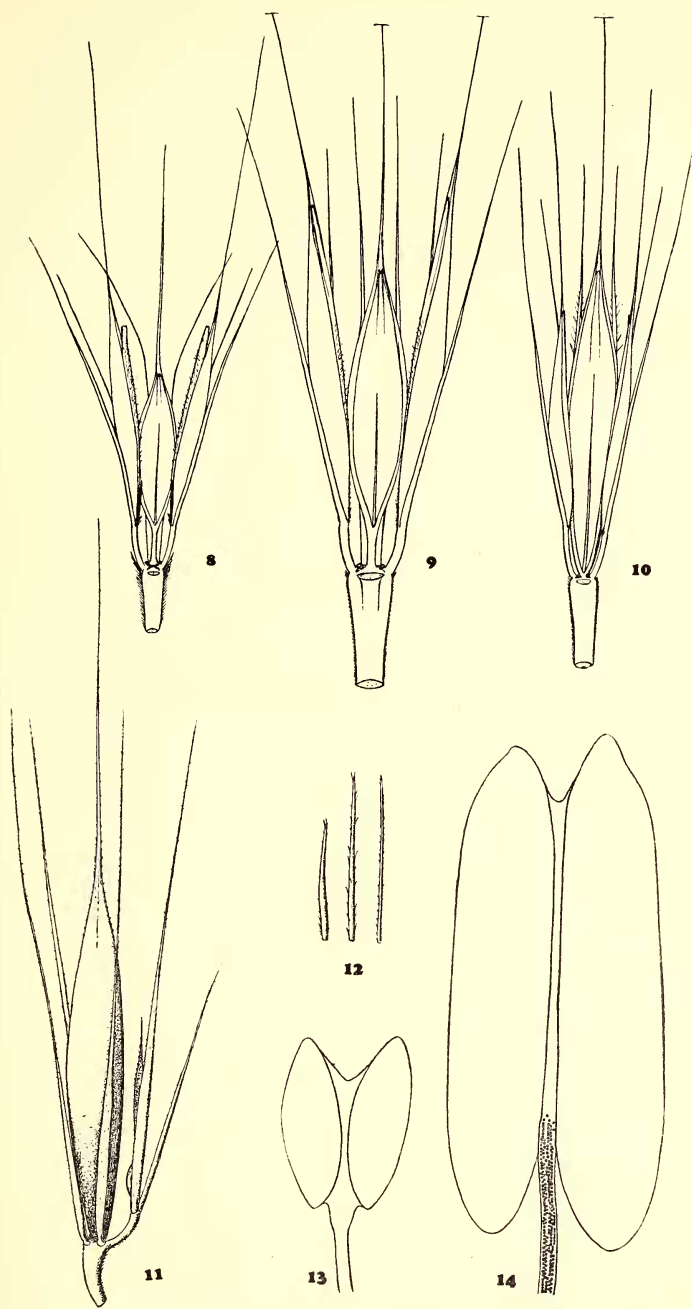


PLATE 2. NORTH AMERICAN SPECIES OF HORDEUM.

are conspicuous morphological differences and, conjecturally, there are no direct phylogenetic relationships between the two entities. *Hordeum brachyantherum* is closely related to *H. californicum* and sometimes it is difficult to separate the two species, while *H. nodosum* seems to be related to Asiatic species like *H. turkestanicum* Nevski and *H. Bogdani* Wilensky. The main morphological difference between *H. brachyantherum* and *H. nodosum* is found in the elongate epidermal cells of the leaf blade, which have straight walls in the first species and undulate walls in *H. nodosum*. This last character also was observed in *H. turkestanicum* Nevski, from central Asia, *H. stenostachys* Godron, of South America, and two apparently undescribed species from Argentina. For other differential characters see key and table 2. Specimens were seen from New Mexico, Arizona, California, Nevada, Utah, Colorado, Oregon, Idaho, Wyoming, Washington, Montana, British Columbia, Labrador, Newfoundland, Alaska, Aleutian Islands. To this species belong also the specimens from Mississippi: Starkville, *Tracy* 279 (US) and from Maine: North Berwick, *Parlin* 1556 (US). In these localities *H. brachyantherum* must be regarded as an introduced species.

3. *HORDEUM JUBATUM* L. Sp. Pl. 85, 1753. "Habitat in Canada." *Critesion geniculatum* Raf. in Jour. Phys. 89: 103. 1819. *Critesion jubatum* (L.) Nevski in Komarov, Flora U.R.S.S. 2:721. 1934.

Nevski (l.c.) separates this species in the monotypic genus *Critesion* Raf. characterized by the very long, capillary, glumes and awns. It is not possible to support this segregation, for there are species and forms with glumes and awns of intermediate length between those of *H. jubatum* and the short awned species; such is the case of *H. comosum* Presl and *H. jubatum* L. var. *caespitosum* (Scribn.) Hitchcock. There are no other characters for separating the two genera.

On the basis of morphological characters, *H. jubatum* shows a close relationship with *H. comosum* Presl, a diploid species from the Andes of South America which is possibly one of the ancestors of *H. jubatum* (a tetraploid species); the other parent would be a species related to *H. californicum*.

3a. *H. JUBATUM* L. var. *CAESPITOSUM* (Scribn.) Hitchcock in Proc. Biol. Soc. Washington 41: 160. 1928. *H. caespitosum* Scribn. in Davenport Acad. Sci. Proc. 7: 245. 1899. Type locality: Geranium Park, Wyoming, ex Hitchcock 1935: 871. *H. adscendens* H.B.K., Nov. Gen. & Sp. 1: 180. 1816. Type locality: "... convalli Mexicana inter montem Chapultepec et Carpio."

This variety differs from the type only in having shorter awns and glumes (1.8–3.5 cm. long), but intermediate forms are found. According to the size of pollen grains and stomata, this form is also tetraploid.

The type of *H. adscendens* H.B.K. was not seen, but the speci-

mens from central Mexico agree with the description of this species and are very similar to the forms growing in the central and western United States, which have been identified as *H. jubatum* var. *caespitosum*. *Hordeum adscendens* H.B.K. was described as an annual species; perhaps this statement is inaccurate, although it is possible that in arid regions the plants, potentially perennials, behave as annuals.

Hordeum jubatum var. *caespitosum* seems to be an entity intermediate between *H. jubatum* and *H. brachyantherum* and it is not improbable that this variety has evolved from the hybridization of these species, whose areas overlap in west and midwest United States and in Canada.

Representative specimens. MEXICO. Xochimilco, *Hitchcock* (US 1019072, pro parte); Rancho Posadas, près de Puebla, *Nicholas* (US 566882), *Arsène* 2285 (US), and *Nicholas* and *Arsène* 76 (US); Prov. San Luis, *Virlet* 1422 (US). UNITED STATES. NEW MEXICO. 2 miles east of Aragon, *Goddard* 832 (UC). NEVADA. Washoe County: Sparks, *Kennedy* 3055 (DS). COLORADO. Montrose County: Paradox, *Walker* 195 (GH); Golden, *Jones* (DS 172272 and 163832). WYOMING. Bitter Creek, *Nelson* 3692 (GH); Point of Rocks, *Merrill* and *Wilcox* 19 (UC). WASHINGTON. Douglas County: Orondo to Waterville, *Benson* 1605 (DS); without loc., *Sandberg* and *Leiberg* 245 (DS, UC). MONTANA. Bozeman, *Blankinship* 608a (DS, UC).

4. HORDEUM MARINUM Huds. Fl. Angl. ed. 2, 1: 127, 1778. *H. maritimum* With. Bot. Arr. Veg. Brit. ed. 2, 1: 27, 1787.

This species and the following one, *H. Hystrix* Roth, are two closely related entities native to the Old World and naturalized in North America, although *H. Hystrix* is widespread while *H. marinum* was found only in eastern United States.

Specimen examined. NEW JERSEY. Camden, in ballast, *Scribner* 776 (UC). This specimen was cited tacitly by *Hitchcock* (1935: 266).

5. HORDEUM HYSTRIX Roth, Catalecta bot. 1: 23. 1797. *H. Gussonianum* Parl. Fl. Paler. 1: 256. 1845. *H. maritimum* With. subsp. *Gussonianum* (Parl.) Asch. et Graeb. Synop. Mitteleurop. Fl. 2: 737. 1902.

This entity differs from *H. marinum* Huds. only in having the inner glumes of the lateral spikelets not broadened, but specimens with intermediate forms are sometimes found. Only cytogenetic evidence can decide whether the two entities are or are not conspecific.

6. HORDEUM PUSILLUM Nutt. Gen. Plant. 1: 87. 1818. "On the arid and saline plains of the Missouri."

Extremely variable species which grows from northern United States to central Argentina. A form growing in southwestern

California and northern Baja California is characterized by having a very broad rachis, the outer lateral glumes also broadened, glumes of the central spikelet narrower and culms with pubescent nodes. This probably is a different ecospecies. The size of the stomata and pollen grains indicates that, like the typical form, it has the diploid chromosome number. A representative specimen is: Baja California, 20 miles south of Tia Juana, *Wiggins 5130* (DS, UC).

One specimen (Arizona, near Granite Reef Dam, *Gillespie 55935* DS, UC), seems to correspond to a tetraploid form, on the basis of size of stomata and pollen grains.

A form with pubescent lemmas was described by Hitchcock as var. *pubens* (Jour. Wash. Acad. Sci. 23: 453. 1933).

7. *HORDEUM DEPRESSUM* Rydb. in Bull. Torrey Bot. Club, 36: 539. 1909. Based on *H. nodosum* L. var. *depressum* Scribn. & Smith in U. S. Div. Agrost. Bull. 4: 24. 1897. *H. Gussonianum* Hitchcock (1935: 266) non Parl., pro parte. Type locality: near Lexington, Oregon.

Hitchcock, in Jepson's "Manual of Flowering Plants of California" (1923: 106) considered this species to be a valid entity, but subsequently (1935: 266) included it in *H. Gussonianum* Parl. (*H. Hystrix* Roth). The two species are clearly different (see key) and, in addition, *H. depressum* is a tetraploid while *H. Hystrix* is diploid.

The chromosome complement of this species (pl. 1, fig. 7) shows one pair of chromosomes with small, spherical satellites and one pair with elongate satellites. The same pattern was observed in *H. brachyantherum*.

The morphological characters of *H. depressum* provide a good basis for the assumption that this species is an allopolyploid involving *H. californicum* and *H. pusillum*, or other species closely related to these (see table 3).

Several specimens from California, Mount Pinos region (*Dudley and Lamb, 4456, 4628, 4710*, DS) show characters intermediate between *H. californicum* and *H. depressum*. They are diploids, according to the size of stomata and pollen grains, have partially sterile pollen and apparently are annuals. Perhaps they have evolved from the cross of *H. californicum* and *H. pusillum* without further polyploidy.

Representative specimens. CALIFORNIA. Orange County: Laguna Beach, *Munz 2192* (DS). Santa Barbara County: vicinity of Prisoner's Harbor, Santa Cruz Island, *Abrams and Wiggins 125* (DS, UC). Ventura County: 10 miles south of Oxnard, *Beetle 3076* (UC-D). Kern County: 6 miles east of Lost Hills, *Beetle 3265* (UC-D). San Luis Obispo County: 8 miles northwest of San Luis Obispo, *Wiggins 3597* (DS). Tulare County: near Earlimart, *Howell 24278* (CAS); near Terrabella, *Beetle 4236* (UC-D). Kings

TABLE 3. DIFFERENTIATING CHARACTERISTICS OF HORDEUM DEPRESSUM, HORDEUM ARIZONICUM, AND THEIR RELATED SPECIES

	<i>H. californicum</i>	<i>H. depressum</i>	<i>H. pusillum</i>	<i>H. arizonicum</i>	<i>H. jubatum</i>
Chromosome number (2n)	14	28	14	42 (?)	28
Habit	Perennial	Annual	Annual	Annual	Perennial
Ratio (length of glumes of central spikelet/length of palea)	1.5-2.5	1.2-2.0	1.2-1.7	2.5-3.5	5-12
Length of lemma of central spikelet, including awn (mm.)	12-22	10-18	10-15	26-32	40-80
Width of { central inner lateral glumes (mm.) } outer lateral	0.08-0.20 0.08-0.18 0.08-0.18	0.20-0.35 0.20-0.45 0.15-0.30	0.40-1.20 0.60-1.70 0.20-0.40	0.20-0.30 0.40-0.50 0.25	0.08-0.18 0.08-0.20 0.07-0.18
Pedicels of lateral spikelets	Usually straight	Usually straight	Curved	Curved	Curved
Lemma of lateral floret	Usually subulate	Acute, awnless	Acute, awnless	Acuminate, shortly pointed	Acuminate, shortly awned (2-6mm.)
Modal length of stomata (μ)	30-44	42-48	29-35	56-64	40-46
Modal diameter of pollen grains (μ)	32-36	43-50	33-36	60-68	42-48

County: 4 miles south of Armona, *Beetle* 2972 (UC-D). Monterey County: Castroville, *Beetle* 4375 (UC-D). Contra Costa County: near Concord, *Kennedy* 4831 (UC-D). San Joaquin County: Durham Ferry Road, *Stanford* 1260 (CAS). Yolo County: Woodland, *Beetle* 4375 (UC-D). Lake County: 2½ miles northeast of Middletown, *Stebbins* and *Covas* 3925 (UC). Colusa County: 4 miles east of Williams, *Ferris* 518 (DS). OREGON. Morrow County: near Lexington, *Leiberg* 39 (GH, UC), isotype of *H. nodosum* var. *depressum*. IDAHO. Nez Perce County: Lewiston, *Henderson* 2845 (US); about Lewiston, *A. A.* and *E. G. Heller* 3025 (UC). WASHINGTON, Kitsap County: Keyport, *Otis* 1612 (DS). Whatcom County: Point Francis, *Muenschner* 8980 (GH). BRITISH COLUMBIA. Vancouver Island: vicinity of Victoria, *Macoun* 222 (GH).

8. *Hordeum arizonicum* Covas sp. nov. *H. adscendens* Hitchcock non H. B. K.

Annun; culmi erecti vel basi geniculati, 30–70 cm. alti. Folia glauca; vaginae inferiores pilosae vel ciliatae, superiores glabrae; ligula truncata 1–2.5 mm. longa; lamina 5–15 cm. longa, 3–6 mm. lata, subtus ciliato-scabra, supra pilosulo-scabra, basi exauriculata. Spica 6–12 cm. longa, 6.5–8 mm. lata aristis non computatis, articulis rachiae margine ciliatis. Terniorum spicula intermedia sessilis, 26–32 mm. longa aristis computatis; glumae lineari-subulatae, 22–26 mm. longae, 0.2–0.3 mm. latae, hispidulo-scabrae; glumella glabra, papulosa, in aristam 17–20 mm. longa attenuata. Spicula laterales pedicellatae, neutrae, pedicellis curvatus, 1–1.5 mm. longis; gluma interiore lineari-subulata, hispidulo-scabra, 19–25 mm. longa, 0.4–0.5 mm. lata, exteriore lineari-setacea, 0.25 mm. lata; glumella subulata, 6–7.5 mm. longa, in acumen capillare 1–2 mm. longum attenuata. Chromosomae $2n = 42$ (?).

Annual with erect culms sometimes geniculate at base, 25–70 cm. tall. Leaves glaucous, the basal ones with hairy, sometimes ciliate sheaths; upper leaves with glabrous sheaths; auricles wanting or vestigial; ligule truncate, 1–2.5 mm. long; blade 5–15 cm. long, 3–6 mm. wide, shortly ciliate-scabrous on the nerves of under side and shortly pubescent-scabrous on the upper side; elongate epidermal cells of the leaf blade with straight walls. Spike 6–12 cm. long, 6.5–8 mm. wide excluding awns; rachis articulate, with almost rectangular segments 1.5–2 mm. long, 0.6–0.9 mm. wide, the margins shortly ciliate. Central spikelet sessile, 26–32 mm. long including awn; glumes linear-subulate, 22–26 mm. long, 0.2–0.3 mm. wide, conspicuously hispid-scabrous; lemma glabrous on the dorsal side, papillose, somewhat scabrous toward apex, tapering into an awn 17–20 mm. long; palea about 8 mm. long, papillose, scabrous toward apex and pubescent on the upper middle of ventral side; rachilla shortly hispid-scabrous, longer than the middle of palea. Lateral spikelets on curved pedicels 1–1.5 mm. long; inner glumes linear-subulate, very sca-

brous, 19–25 mm. long, 0.4–0.5 mm. wide; outer glumes linear-setaceous, about 0.25 mm. wide; lemmas subulate, 6–7.5 mm. long, with acuminate apex scarcely awned. Modal diameter of pollen grains 60–68 μ . Modal length of stomata 58–64 μ . Hexaploid (?)

Type. Fort Lowell, Arizona *J. J. Thornber 536* (US; isotypes, DS, UC).

Specimens examined. ARIZONA: Santa Cruz bottoms, *Griffiths 2709* (US) and *4063* (US). Phoenix, *Williams 3029* (US) and *Gould 3516* (UC). Sacaton, *Peebles* and *Harrison 1636* (US). West of Apache Junction, *Silveus 2672* (US). Mission Pool, Tucson, *Benson 9392* (DS, UC). Fort Lowell, *Thornber 404* and *538* (US). CALIFORNIA: United States Yuma Field Station, *Bard, Reeder 21* (US).

This new species was referred by Hitchcock (1935: 268) to *H. adscendens* H.B.K. which is a synonym of *H. jubatum* var. *caespitosum*; this variety differs from *H. arizonicum* in the perennial habit, the leaves scabrous, the glumes setaceous less than 0.2 mm. wide and in being a tetraploid, while *H. arizonicum*, according to the size of pollen grains and stomata, is a high polyploid, perhaps a hexaploid which probably has evolved from the cross of *H. jubatum* (tetraploid) and *H. pusillum* (diploid), as is suggested by the morphological characters (see table 3).

9. *Hordeum Stebbinsii* Covas, sp. nov. *H. murinum* auct. non L., pro parte. *H. murinum* L. var. *pedicellatum* Pau et Font Quer in Font Quer, *Iter maroc.* no. 96. 1927.

Annum; culmi erecti vel adscendentes, 10–50 cm. alti. Folia glauca; vaginae glabrae; ligula truncata 0.8–1.5 mm. longa; lamina sparse pilosa, 2.5–7 mm. lata, basi auriculata; auriculae 1–3 mm. longae. Spica ovato-oblonga, densissima, 4–9 cm. longa, 6–10 mm. lata aristis non computatis; articulis rachiae margine ciliatis. Terniorum spicula intermedia sessilis; glumae lineari-lanceolatae, scabrae, utrinque ciliatae, 12–22 mm. longae, 0.3–0.5 mm. latae; flosculo stipitato; glumella glabrae, in parte superiore scabra, in aristam 8–25 mm. longam acuminata; palea 5–9 mm. longa, lateralium $\frac{3}{4}$ partes aequans; antherae 0.2–0.5 mm. longae. Spicula laterales pedicellatae, neutrae vel masculae, gluma interiore lineari-lanceolata, scabrae, utrinque ciliatae, 0.3–0.5 mm. lata, exterior lineari-subulata, 0.2–0.3 mm. lata; glumella in parte superiore scabra, in aristam acuminata, arista reliquas aristas superante; palea utrinque pilosa, 7–10 mm. longa. Chromosomae $n = 7$.

Annual, with erect or ascending culms, often pruinose, 10–50 cm. tall. Leaves glaucous with smooth sheaths; blades usually sparsely pubescent, 2.5–7 mm. wide, auriculate at base; auricles 1–3 mm. long; ligule truncate 0.8–1.5 mm. long. Spike ovate-oblong, 4–9 cm., 6–10 mm. wide excluding awns, very dense (6–8

spikelets per cm. of rachis), the apical spikelets with shorter awns than the central or basal ones; segments of rachis ciliate at margins; cilia 0.25–0.75 mm. long, gradually shorter toward the base of segments. Central spikelet 16–36 mm. long including awn, sessile; glumes linear-lanceolate, 3-nerved, 12–22 mm. long, 0.3–0.5 mm. wide, with long cilia on both margins; floret pedicelled, the pedicel 1.2–1.7 mm. long, as long as the pedicels of lateral spikelets; lemma glabrous, scabrous only on the nerves near apex, tapering into an awn 8–25 mm. long; palea 5–9 mm. long, glabrous inside, sparsely pubescent between the nerves outside, about $\frac{3}{4}$ times as long as the paleas of lateral florets; anthers very small, included at anthesis, 0.2–0.5 mm. long, with entire or shortly bilobed base; filament 0.7–0.9 mm. long, broadened at apex, without conspicuous starch grains; prolongation of rachilla setaceous, scabrous, 3–4 mm. long. Lateral spikelets on a slender pedicel 1.2–1.7 mm. long, ciliate inside; inner glumes linear-lanceolate, similar to the central ones; outer glumes linear-subulate, 0.2–0.3 mm. wide; florets usually neuter, sometimes staminate, more developed than the central fertile floret; lemmas scabrous toward apex, tapering into an awn longer than that of central lemma; palea ciliate-pubescent on both sides, scabrous on the nerves near the notched apex, 7–10 mm. long; stamens, when fertile, exerted at anthesis, with anthers somewhat larger than those of central floret; prolongation of rachilla subulate, stout, scabrous, 1.0–2.2 mm. long, usually orange colored at maturity. Modal diameter of pollen grains 33–38 μ . Modal length of stomata 32–38 μ . Chromosome number $n = 7$ (fig. 6).

Type. Roadside weed, 5 miles southeast of Middletown, Lake County, California, May 9, 1948, *G. L. Stebbins* and *G. Covas* 3927 (UC 754601; isotypes, NY, GH, DS, UC-D).

Specimens examined Morocco. Marsa Saguira, *Font Quer* 96 (UC), isotype of *H. murinum* var. *pedicellatum*. EGYPT. Damietta, *Ehrhenberg* (UC 330933). MEXICO. Baja California: San Antonio, *Brandegge* 82 (UC). UNITED STATES. ARIZONA. Tucson, *Thornber* (UC 33927); Wickenburg, *Jones* (UC 407728). Tempe, Maricopa County, *Gillespie* 5589 (UC). CALIFORNIA. San Diego County: Warner's Ranch, *Hall* 6465 (UC); 3 miles west of Dulzura, *Wiggins* 2191 (UC). Los Angeles County: Santa Catalina Island, *Brandegge* (UC 120595); San Clemente Island, *Munz* 6620 (UC). Santa Barbara County: Santa Cruz Island, *Brandegge* (UC 185567). Riverside County: Thomas Ranch, *Hall* 2176 (UC). Tulare County: Tulare, *Loughridge* (UC 38658). Monterey County: Capitola, *Stebbins* 3941 (UC, GH, US); 11 miles west of Soledad, *Stebbins* 3948 (UC, GH, UC-D, US). Fresno County: Pine Ridge, *Hall* and *Chandler* 306 (UC). Stanislaus County: Adobe Valley, Mount Hamilton Range, *Sharsmith* 3539 (UC). Lake County: 2 $\frac{1}{2}$ miles northeast of Middletown, *Stebbins* and *Covas* 3951 (UC, GH, NY, UC-D, US). Glenn

County: near Norman, *Burt-Davy 4292* (UC). NEVADA: between Glendale and Burkerville, *Maguire* and *Blood 1302* (UC). ARGENTINA. Mendoza: Lujan, Potrerillos, *Semper 8242* (Leal); Las Heras, La Crucesita, *Semper 4160* (Leal); Godoy Cruz, *Ruiz Leal 3344* (Leal); Tunuyan, Real de las Cuevas, *Ruiz Leal 3186*

TABLE 4. DIFFERENTIATING CHARACTERISTICS OF *HORDEUM STEBBINSII*, *HORDEUM LEPORINUM*, AND *HORDEUM MURINUM*

	<i>H. Stebbinsii</i>	<i>H. leporinum</i>	<i>H. murinum</i>
Chromosome number (2n)	14	28	14
Density of spike (spikelets per cm. of rachis)	6-8	3-5	3-6
Length of the cilia on the margins of the segments of the rachis (mm.)	0.25-0.75	0.10-0.30	0.10-0.30
Floret of the central spikelet	Pedicellate	Pedicellate, sometimes sub-sessile	Sessile or sub-sessile
Ratio (width of glume of central spikelet/width of inner glume of lateral spikelet)	1	1-1.3	1.4-2
Ratio (length of central palea/length of lateral paleas)	0.7-0.8	0.7-0.9	1.0-1.4
Anthers of central floret	Base entire or shortly bilobed; 0.2-0.5 mm. long	Base strongly bilobed; 0.8-1.5 mm. long	Base strongly bilobed; 0.7-1.0 mm. long
Filaments of stamens	Without starch grains	With starch grains	With starch grains ¹
Prolongation of rachilla of lateral spikelets	Stout, often orange-colored, 1.0-2.2 mm. long	Intermediate, 2.8-3.7 mm. long	Setaceous, not colored, 2.2-3.1 mm. long
Palea of lateral floret	Pubescent	Pubescent, sometimes glabrous toward apex	Almost glabrous

¹ This character was observed also in *H. vulgare*, *H. bulbosum*, *H. marinum*, and *H. Hystrix*.

(Leal). For this species only the material in the Herbarium of the University of California and in that of Mr. A. Ruiz Leal (Mendoza, Argentina) has been studied.

I am glad to give to this species the name of Dr. G. L. Stebbins Jr., who recognized diploid and tetraploid forms in the complex which comprised this new species and *H. leporinum* Link (see discussion on the following species).

10. *HORDEUM MURINUM* L. Sp. Pl. 85. 1753. "Habitat in Europae locis ruderalis." *H. ciliatum* Gilib.?, Excert. Phyt. 2: 520. 1792.

This species, together with *H. leporinum* Link and *H. Stebbinsii* Covas, forms a complex which often has been classified as *H. murinum* L. Some authors recognized *H. leporinum* as a subspecies of *H. murinum*, while Nevski (1934: 726) and Parodi (1941: 9) give specific status to Link's entity.

Hordeum murinum seems to be a mesophytic species of cool-temperate regions while *H. Stebbinsii* is rather xerophytic, growing in warm-temperate regions. Both species are diploid and although they are closely related do not overlap in many of the differential characters. On the other hand, *H. leporinum* is a more vigorous species growing in intermediate habitats and with morphological characters which often overlap either those of *H. murinum* or *H. Stebbinsii* (see table 4). *H. leporinum*, being a tetraploid species, can then be regarded as an allopolyploid derived from *H. murinum* and *H. Stebbinsii*, which originated probably in the Mediterranean region, where the areas of the parental species come together.

Specimen examined. WASHINGTON. Clallam County: Dungeness, W. C. and M. W. Muenscher 5658 (UC). Other specimens were seen from Europe. (For this species only the material in the Herbarium of the University of California has been studied.)

11. *HORDEUM LEPORINUM* Link in Linnaea 9: 133. 1835. "Frequens in Graecia." *H. murinum* L. subsp. *leporinum* (Link) Aschers. et Graebn. Synop. Mitteleurop. Fl. 2(1): 739. 1902. *H. ambiguum* Doell in Martius, Fl. Bras. 2(3): 231, t. 57. 1880.

The North American material classified as *H. murinum* L. is mostly *H. leporinum* Link. This species shows great variability, mainly in quantitative characters, but ordinarily it is not difficult to recognize *H. leporinum* and its two probable parents, *H. murinum* and *H. Stebbinsii*.

12. *HORDEUM VULGARE* L. Sp. Pl. 84. 1753.

The common barley (f. *hexastichon*) can be considered a naturalized species at least in certain districts of California, where it grows in almost pure stands on the roadside, mainly in slightly alkaline soils.

SPECIES EXCLUDED

HORDEUM NODOSUM L. Sp. Pl. ed. 2: 126. 1762, "Habitat in Italia, Anglia." *H. secalinum* Schreb., Spicil. Fl. Lips. 148. 1771. The North American specimens referred to this species are either *H. brachyantherum* Nevski or *H. californicum* Covas and Stebbins (see discussion on these species).

HORDEUM MONTANENSE Scribn. in Beal, Grasses N. Am. 2: 644, 1896. *Hordeum Pammelii* Scribn. & Ball, Iowa Geol. Surv. Suppl. Rep. 1903: 335, 1904. This entity is quite probably a sterile intergeneric hybrid involving *Hordeum jubatum* L. and *Elymus virginicus* L. The material examined shows 100 per cent pollen sterility and no seeds or developing ovaries were found. Specimens examined. WYOMING. *Griffiths 930* (US). ILLINOIS. Stark County: 2½ miles north of Wady Petra, *Chase 1919* (US); *Chase 45* (US).

Also the following specimens are presumably intergeneric hybrids which have been given no taxonomic designation: OREGON. Hot lake, *Piper* (US 1107887), probably *H. jubatum* L. x *Elymus triticoides* Buckl. SOUTH DAKOTA. Brookings, *Jarvis* (US 730679), probably *H. jubatum* L. x *Elymus canadensis* L. NOVA SCOTIA. Colchester County: Lower Onslow, *Roland 41076* (GH), probably *H. jubatum* L. x *Elymus* sp.

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